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Adaptyxis n.gen. (Umboniidae, Nerineacea, Gastropoda) from the Mirdita Zone of Albania; remarks on the early phylogeny of the Nerineacea

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(With 2 plates)

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Summary

Based on material from the Barremian/Aptian of Albania, the nerineacean *Adaptyxis* n. gen. is described. It possesses high turriculate shells with concave whorls of moderate height. Because of the hollow columella it is assigned to the Umboniidae LYSSENKO & ALIEV. The columella is hollow. Of the internal plaits, the adapical columellar plait is very small. The other columellar plait, the palatal plait and the parietal plait are strong. Because of the internal morphology, *Adaptyxis* is considered as transitional between the genus *Affiniptyxis* LYSSENKO & ALIEV and *Plesioplocus* PCHELINTSEV. Synchronously, *Neoptyxis* PCHELINTSEV evolved from *Affiniptyxis*. Both genera are part of the Simploptyxidae HAKOBJAN. An origin of the Umboniidae and the Ptygmatidae from a *Melanioptyxis*-like group in the Jurassic is considered. It is not clear whether the Nerineidae originated from the same group as the other nerineacean families or from the Mathildoid family Anoptychoidae, as was postulated by BANDEL (1995).

Zusammenfassung

Aufgrund von Material aus dem Barremium/Aptium Albaniens wird die Gattung *Adaptyxis* n.gen. beschrieben. Vertreter dieser Gattung besitzen hohe, turrikulate Gehäuse mit mäßig hohen, konkaven Umgängen. Die Columella ist breit und hohl. Unter den Internfalten ist die adapikale Columellafalte sehr klein. Die andere Columellarfalte, sowei die Parietal- und Palatalfalte sind kräftig. Wegen der hohlen Spindel sowie der Anzahl und der Größenverhältnisse der Internfalten wird *Adaptyxis* als evolutives Zwischenglied von der zu den Umboniidae gehörigen Gattung *Affiniptyxis* LYSSENKO & ALIEV zu *Plesioplocus* angenommen. Die Differenzierung zwischen *Plesioplocus* PCHELINTSEV und *Neoptyxis* PCHELINTSEV erfolgte in einem frühen Stadium des Übergangs. Beide Gattungen gehören der Familie Simploptyxidae HAKOBJAN an. Der Ursprung der Umboniidae und der Ptygmatidae von einer mit *Melanioptyxis* nahe verwandten Gruppe wird diskutiert. Es ist unklar, ob der Ursprung der Familie Nerineidae in der selben Gruppe liegt oder ob sie von der den Mathildoidea angehörigen Familie Anoptychoidae abstammt, wie es von BANDEL (1995) angenommen wird.

1. Introduction

In Upper Cretaceous nerineaceans the columella is solid or possesses only narrow cavities. This applies to the Nerineidae including the Nerinellidae and the Simploptyxidae

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HAKOBJAN (1976). The Eunerineidae, with *Eunerinea* COX (*Nerinea* DEFRANCE in COSSMANN, 1896 and others) and *Diptyxis* OPPENHEIM, possess a single columellar plait. Representatives of the Simploptyxidae have two columellar plaits. HAKOBJAN (1976) considered *Plesioplocus* PCHELINTSEV, *Simploptyxis* TIEDT, *Parasimploptyxis* HAKOBJAN, *Haploptyxis* HAKOBJAN, and *Plesioptygmatis* BOESE as members of this family. According to HAKOBJAN, all other genera evolved from *Plesioplocus*, which itself had its origin in the "Diozoptyxisidae" in the sense of PCHELINTSEV (1931, 1965). *Neoptyxis* was not included into the Simploptyxidae by HAKOBJAN.

In the Mirdita Zone of Albania, nerineaceans with morphological characters of both the Umboniidae and the Simploptyxidae have been found by PEZA and his co-workers. They therefore provide direct evidence on the origin of the Simplopyxidae as it was assumed by HAKOBJAN. This material, which does not correspond to any of the known nerineacean genera, is described in the present paper.

2. Geological setting

The nerineacean material was collected on the Buzemadhe hill in the vicinity of the villages Lavdar and Gjonomadh (Voskopoja region) west of the town of Korca, southeast Albania (Fig. 1). Tectonically, the area is part of the Mirdita zone (see PEZA 1989). The Buzemadhe hill (Fig. 2) consists of deposits of Barremian to Aptian age. They overlie series of tightly folded ophiolitic rocks (Fig. 2, series 1) and of great fractured blocks of Triassic-Jurassic carbonates (PEZA 1988). From base to top the Cretaceous series of the Buzemadhe hill consists of the following sediments (PEZA 1988):

2. – 50 m of alternating conglomerates and sandstones. They overlie the ophiolites transgressively. The clasts consist mainly of ophiolitic material of variable grain size. A small portion of the clasts was derived from the Triassic-Jurassic limestones which are widely spread in the pre-Cretaceous series of the Voskopoja region. Except for *Adaptyxis lavdaris* n. gen. n. sp., molluscs are rare. The following fauna has been recorded in the sandstones and conglomerates (after PEZA 1988, modified): *Caprina varians* PAQUIER, *Neithea atava* (ROEMER), *Neithea morrisi* (PICTET & RENEVIER), ?*Nerinella mutabilis* (DELPEY), aff. *Neoptyxis galeata* (COQUAND, see chapter 5.1.), *Multiptyxis dayi* (BLANCKENHORN), *Aptyxiella fraasi* (BOEHM), *Orbitolina* sp. This assemblage is characteristic for the Urgonian facies of Barremian – Aptian age (PEZA 1988).

3. – 30 m of pink conglomeratic limestones. As in the underlying beds, clasts were derived from ophiolitic rocks and Triassic – Jurassic limestones. The pink colour originates from ophiolitic material and fragments of ferruginous rocks.

4. – 115 m of well-bedded pink limestones containing *Orbitolina*. This series forms the top of the Buzemadhe hill.

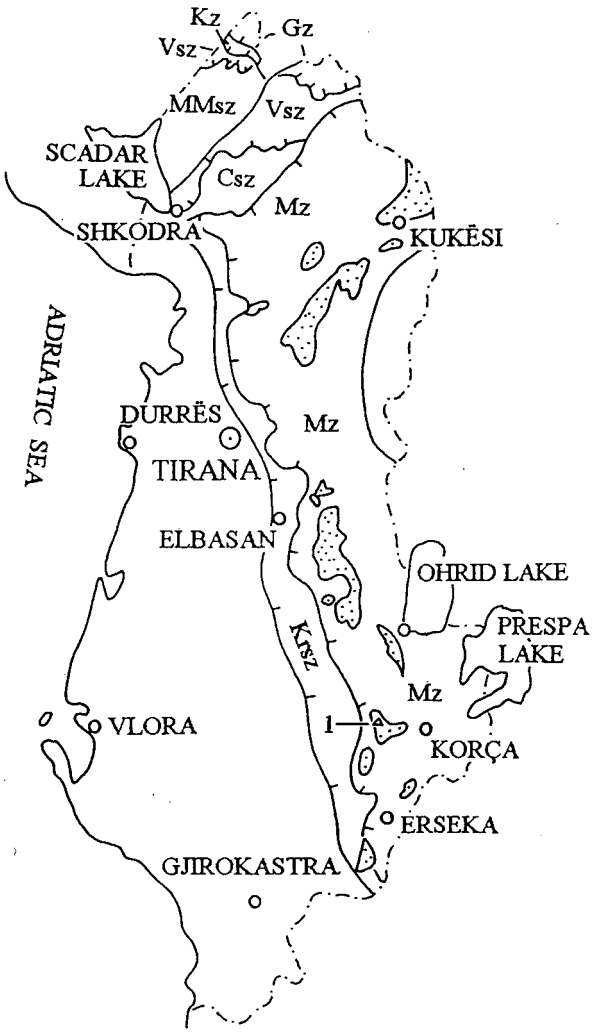

Fig. 1. The distribution of Cretaceous rocks (dotted) in the Mirdita zone of Albania (MZ). 1: Position of the Buzemadhe hill, close to Lavdar and Gjonomadh. For other tectonic zones see PEZA (1989).

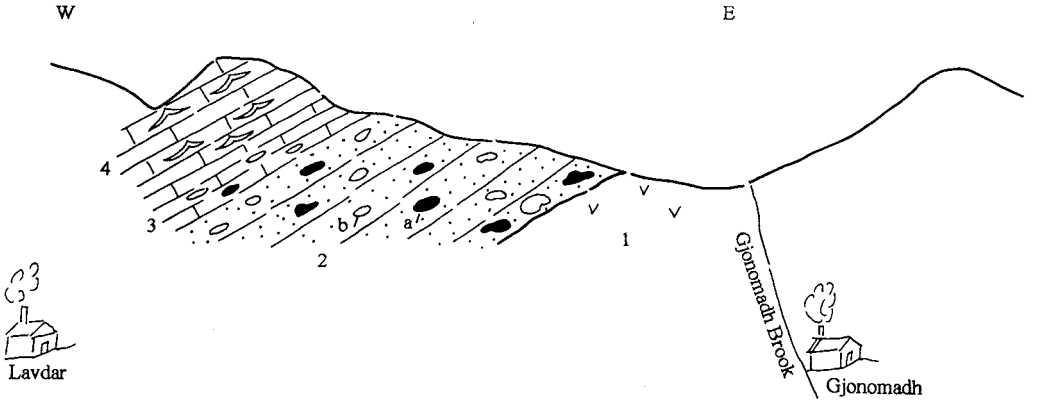

Fig. 2. Section through the Cretaceous of the Buzemadhe hill. The numbers correspond to the description in the text.

3. Systematic description

Superfamily Nerineacea

Family Umboniidae LYSSENKO & ALIEV, 1987

Synonym: Dioptyxisidae PCHELINTSEV, 1965

Remarks. The genus *Diozoptyxis* with *Nerinea monilifera* d'ORBIGNY as type species was established by COSSMANN (1896). Based on the description in the Paléontologie Francaise by d'ORBIGNY (1842), COSSMANN incorrectly assumes two columellar plaits and a palatal plait in the type species. It was already mentioned by OPPENHEIM, 1906, that this was not the case. DELPEY (1941–42) assigned *Diozoptyxis* to the Campanilidae. The description was revised by KOLLMANN (1987) after investigating d'ORBIGNY's type material, which is kept in the collection GUERANGER. It was shown that *Nerinea monilifera* possesses a single columellar plait which is developed only in the last whorl. This agrees with other Cretaceous Campanilidae.

Based on COSSMANN's (1896) description of three internal plaits, PCHELINTSEV (1931) included species with broadly hollow columellas into *Diozoptyxis*. Later, PCHELINTSEV (1965) accepted that the systematic position of *Nerinea monilifera* within the nerineacea cannot be upheld. He replaced *Nerinea monilifera* by *Nerinea renauxiana* as type species of *Diozoptyxis*. In the same monograph, he established a family Dizoptyxisidae. It contained *Diozoptyxis* in the new sense and the new genus *Umbonea*. VAUGHAN (1988) quoted DELPEY (1941–42) that *Nerinea monilifera* d'ORBIGNY is a Campanilidae gastropod. Nevertheless, she upheld the genus *Diozoptyxis* in the sense of COSSMANN and PCHELINTSEV by referring to Article 70c of the ICZN of 1985. MUSTAFA & BANDEL, 1992 followed this argumentation.

We do not agree with this interpretation. Article 70c applies to the case in which an author fixes explicitly "as the type species of a new nominal genus or subgenus a previously established nominal species but states that its name is used in the sense of the misidentification or misapplication of a previous author" (quotation). This is definitely not the case with *Diozoptyxis*, which was established by COSSMANN on a species which was correctly described by d'ORBIGNY. Therefore, the generic name *Diozoptyxis* cannot be applied to nerineacean gastropods and the family name Diozoptyxisidae is invalid.

Because of this, LYSSENKO & ALIEV (1987) introduced the family Umboniidae instead of the Diozoptyxisidae PCHELINTSEV. These authors assigned the genera *Umbonea* PCHELINTSEV, *Pchelincevia* LYSSENKO & ALIEV and *Affiniptyxis* LYSSENKO & ALIEV to the new family. Evidently the latter two genera replace *Diozoptyxis* in the sense of PCHELINTSEV (1965).

LYSSENKO & ALIEV did not refer to *Adiozoptyxis* DIETRICH (1914). This author had proposed that smooth species should be separated from *Diozoptyxis* in the sense of COSSMANN. For them he introduced the new generic name *Adiozoptyxis*. Referring to the artificiality of this group he did not formally establish this genus but used the name with a question mark. On page 108 of the Fossilium Catalogus, DIETRICH (1925) dealt with *Nerinea polymorpha* GEMMELLARO (1865). He correctly assigned a small specimen described by GEMMELLARO under this name (pl. 2, fig. 3) to *Phaneroptyxis*. Two large

specimens (GEMMELLARO 1865, pl. 2, fig. 4,5) he assigned to *Adiozoptyxis*, which he considered here as a subgenus of *Nerinea*. This means that the species name "*polymorpha*" was kept for both genera, *Phaneroptyxis* and *Adiozoptyxis*. The new subgeneric name cannot even be found in the index of the "Fossilium Catalogus".

DIETRICH has questioned the species name of the specimens which he put into *Adiozoptyxis*. It is therefore obvious that he wanted to apply "*polymorpha*" to the *Phaneroptyxis* species. We do not agree with COX (1954), who interpreted DIETRICH's mentioning of *Adiozoptyxis* in connection with *Nerinea polymorpha* as a designation of a type species. This means that *Adiozoptyxis* does not possess a valid type species and therefore is invalid in the taxonomic sense.

Adaptyxis n. gen.

G e n e r i c n a m e: A composite from adapicalis = close to the apex and ptyxis = plait

D i a g n o s i s o f g e n u s: Highly turriculate Nerineaceans with low, deeply concave whorls. Columella broad, hollow. Large, acute parietal and palatal plaits; 2 columellar plaits; abapical columellar plait large, acute, adapical one small.

T y p e s p e c i e s: *Adaptyxis lavdaris* n.sp.

R e m a r k s: Several species which differ in their whorl shape and sculpture may be assigned to *Adaptyxis* because of the broad central cavity and the small adapical columellar plait additionally to a large one (see below). Because of its broad central cavity and the shape of the whorl, *Adaptyxis* n.gen. is assigned to the Umboniidae LYSSENKO & ALIEV (1987). It differs from *Affiniptyxis* LYSSENKO & ALIEV, *Pchelincevia* LYSSENKO & ALIEV and *Umbonea* PCHELINTSEV by the additional small columellar plait.

In *Affiniptyxis* LYSSENKO & ALIEV (1987) the whorls are broad rhombic in cross section. The base is inclined at an angle of almost 90° towards the shell axis. The columella plait is situated in the abapical third of the the columella which is high. *Pchelintsevia* LYSSENKO & ALIEV and *Umbonea* PCHELINTSEV (1965) have narrow rhombic whorls. They are low in *Pchelintsevia* and high in *Umbonea*. *Pchelintsevia* contains forms which agree with *Adiozoptyxis* DIETRICH (1914). We also include *Fibuloptyxis* PCHELINTSEV (1965) into the Umboniidae. Besides a distinct basal plait which is situated in the external half of the basal wall (see also WIECZOREK 1975), the number and shape of plaits agrees with *Adaptyxis*. It differs from this genus by its very high concave whorls, a more narrow central cavity and the long bent basal processus of the whorls.

Representatives of *Ptygmatis* have the same number of internal plaits. Their whorls are much more restricted internally. The abapical columellar plait is long and bent in an adapical direction. The free end of the plaits is inflated or bifurcate.

Adaptyxis lavdaris n.sp.

(Plate 1, Figures 1 – 6; Plate 2, Figures 7 – 10)

S p e c i e s n a m e: Named after the village of Lavdar in the vicinity of the Buzemadhe hill.

T y p e L o c a l i t y: Buzemadhe hill, southeast Albania.

H o l o t y p e: Plate 1, Fig.1,2; deposited in the Museum of the Geological Institute, Tirana

P a r a t y p o i d s: 28 specimens deposited in the Museum of the Geological Institute, Tirana

D i a g n o s i s o f s p e c i e s: High turriculate; whorls moderately high, concave, irregular tubercles at ababical suture.

D e s c r i p t i o n: The shells are large turriculate. The whorls are moderately high, concave, with deepest incision in the middle. Abapically, the whorls bear irregular tubercles. Axial sections show a broad columella with a wide central cavity. The whorls are broadly rhombic in outline. A central pillar which was formed by a fairly long siphonal neck is only preserved in the holotype. The columellar wall is slightly oblique towards the axis and bears two columellar plaits. The abapical columellar plait is situated between the abapical and middle third. It is strong and slightly bent in an adapical direction. The adapical columellar plait is weak and hardly visible in late ontogenetic whorls. The strong parietal plait is bent with distinct angle in an adapical direction. The palatal plait is broad, prominent, and rounded at its crest. The basal plait is broad and low.

Measurements (in mm).

total height	max.diam.	height of last whorl	tot.height/ max. diam.	spiral angle
81 (fragm.)	41	14	0,34	19°
93 (fragm.)	37	11	0,3	20°
105 (fragm.)	37	11	0,29	18°
95 (fragm.)	35	10	0,28	22°
87 (fragm.)	33	12	0,5	17°
84 (fragm.)	31	10	0,32	20°

Adaptyxis carinatus n.sp.

(Plate 2, Fig. 5 – 8)

S p e c i e s n a m e: From the prominent sutural ridge

T y p e L o c a l i t y: Buzemadhe hill, southeast Albania.

H o l o t y p e: Plate 2, Fig.6. Deposited in the Museum of the Geological Institute, Tirana.

P a r a t y p o i d s: Over 55 specimens, kept in the same collection.

D i a g n o s i s: Large turriculate shells; whorls moderately high, deeply concave, with strong, acute sutural ridge.

D e s c r i p t i o n: The shells are large turriculate. The shell angle is large in early ontogenetic stages. Large growth stages are almost cylindrical. The moderately high whorls are deeply and narrowly constricted. The zone of deepest constriction lies abapically of the middle. The sutural ridges are acute and smooth. The sutures are situated abapically of their crest.

Axial sections show a broad central cavity of the columella. The columellar wall is strongly oblique towards the shell axis. Abapically, it bears a large plait which is bent in

an adapical direction. The adapical columellar plait small. The prominent parietal plait is truncated at the end. The base of the palatal plait is broad and its crest rounded. The basal plait is broad and low.

Measurements.

total height	maximum diameter	height of last whorl	total height/ max. diameter	spiral angle
110	51	15	0,3	14°
121	41	12	0,3	15°
107	43	17	0,37	0°
94	42	17	0,4	0°
130	40	13	0,32	0°
95	38	14	0,39	0°
93	36	12	0,33	11°

D i f f e r e n c e s: *Adaptyxis carinatus* n.sp. differs from *A. lavdaris* by its deeply constricted whorls and the acute prominent sutural ridge.

4. Other species belonging to *Adaptyxis* n.gen.

Nerinea essertensis PICTET & CAMPICHE (1862, p. 242, pl. 69, fig. 1) from Ste. Croix, Switzerland. The whorls are moderately convex and smooth. After PICTET & CAMPICHE, the "coupe paraissant indiquer l'absence d'un ombilic". The internal plaits are acute. The abapical columellar plait is long, the adapical columellar plait small. The parietal plait is long and bent. The palatal plait is short and broad. Age: "Urgonian"

Nerinea prefleuriaui DELPEY (1940). The specimen figured on plate 3, fig. 11 has acute plaits and may belong to *Adaptyxis* n.gen. Other specimens assigned to this species by DELPEY belong to *Ptygmatis*. Age: Aptian

Nerinea cedrorum BLANCKENHORN (1890, p.105, pl. 8, fig.1). The figured specimen has low whorls. They are moderately concave to flat; the angle between the base and the whorl side is almost 90^{o}. The periphery of the last whorl is rounded or bears an indistinct bulge. The sculpture consists of growth lines. Age (after DELPEY 1940): Cenomanian

5. Phylogenetic aspects

5.1. The origin of the Simploptyxidae

HAKOBJAN (1976) postulated the origin of the Simploptyxidae from the Diozoptyxinae (= Diozoptyxisidae PCHELINTSEV, 1965), which have been re-named into Umboniidae by LYSSENKO & ALIEV (1987). The Simploptyxidae have two columellar plaits of which the adapical one is very small or at least smaller than the other one (except for *Plesioptygmatis* BOESE). While the columella is hollow in the Umboniidae it is more or less solid in the Simploptyxidae. Only in very large growth stages of Simploptyxis TIEDT (1958), a wide central cavity does occur. The evolutionary step towards a solid columella is not as abrupt as it may appear. The whorls of Umboniidae species had a

delicate but fairly long siphonal neck which formed a pillar within the columella. In "perfect" axial sections this pillar is completely removed. In oblique sections it is commonly not hit by the cutting plane. Therefore, most axial sections show a broad central cavity of the columella. The closing of the central cavity in *Plesioplocus* is due to a tighter coiling of the whorls. Quite often, hollow portions remained between the former siphonal necks and the columellar walls of the following whorls.

Judging from the number of plaits and from the structure of the columella we agree with HAKOBJAN (1976) that the Simploptyxidae have evolved from the Umboniidae. We believe that *Adaptyxis* occupies an intermediate phylogenetic position. This evolutionary step occurred in the late Barremian/early Aptian.

5.2. Relationship of *Adaptyxis* n.gen. to *Plesioplocus* PCHELINTSEV and *Neoptyxis* PCHELINTSEV

Among the Simploptyxidae, *Plesioplocus* PCHELINTSEV (1953) has a minute adapical columellar plait. It evolved from *Adaptyxis*, which has the same characteristic feature. Stratigraphically, *Plesioplocus* ranges upwards into the Upper Cenomanian.

Neoptyxis PCHELINTSEV (1934) has a larger adapical columellar plait than *Plesioplocus* and was assigned to the Triptyxidae PCHELINTSEV by HAKOBJAN (1976). Because of this small difference to *Plesioplocus*, we consider *Neoptyxis* as a Simploptyxidae genus.

In *Neoptyxis* a comparable step from a hollow to a solid columella occurred as in *Plesioplocus*. *Nerinea galeata* COQUAND (1865), which was re-described by CALZADA (1992) from the Hauterivien of the Iberian Range, possesses a hollow columella but columellar plaits like those of *Neoptyxis*. The spezies was therefore assigned to *Neoptyxis* by CALZADA (1992). Under the same name, DELPEY (1940) has described specimens from the Albian which belong to the same group but to a different species (CALZADA 1992). *Nerinea* sp. aff. *galeata* MONGIN in COMBES & MONGIN (1971) is a genuine *Neoptyxis*. Another species belonging to this group is *Nerinea (Nerinea) sanjuanensis* BUITRÓN & BARCELÓ-DUARTE (1980) from the Aptian of Mexico. The authors have pointed out the close resemblance with *N. galeata* COQUAND.

Obviously, the differentiation between *Plesioplocus* and *Neoptyxis* took place in the early stage of the evolution of the Simploptyxidae. Concerning the phylogenetic origin of the other Simploptyxidae, *Neoptyxis*, with its more prominent adapical plait, seems to be as good a candidate as *Plesioplocus*.

5.3. Origin of the Umboniidae

According to PCHELINTSEV (1965) the "Diozoptyxisidae" first appeard in the Upper Jurassic (Tithonian). Stratigraphically, they range upwards into the Aptian (WIECZOREK & LLOMPART 1994). The most closely related group are the Ptygmatidae. They have the same whorl shape and a more or less broad central cavity of the columella, but differ from *Adaptyxis* by two columellar plaits. They are about equal in size but inflated and furcated towards the end. The Ptygmatidae are already diverse in the Middle Jurassic (COSSMANN 1898). Because of the larger number and the complicated morphology of

plaits it is unlikely that the Umboniidae evolved from of the Ptygmatidae. Nevertheless, they probably evolved from the same group of umbilicate nerineaceans.

As a common ancestor, a nerineacean similar to *Melanioptyxis* COSSMANN (1896) seems possible. This genus has prominent columellar and palatal plaits and a small parietal plait. The central cavity is of medium width. The whorls are fairly high and flat. COSSMANN (1896, 1898) recorded a first occurrence of *Melanioptyxis* in the Bajocian. The ancestry to the Ptygmatidae would imply earlier representatives of this group or related ones.

5.4. Is there a common origin with the Nerineidae?

Nerineidae and early "Nerinellidae" possess a solid columella, one columellar plait, one parietal plait and one palatal plait. Species assigned to the "Nerinellidae" are small and mostly possess high whorls. These characters may also occur in Nerineidae species. Therefore, there is no necessity of separating these families. We do not agree with PCHELINTSEV (1965) who postulates a polyphyletic origin of Nerineidae and "Nerinellidae".

WANNER (1910) has recorded *Nerinea timorensis* together with a fauna of other molluscs from beds which he dated as Liassic (Pliensbachian) (see also KRUMBECK 1923). This dating appears to be somewhat unreliable, but for others a Liassic age has been proved. An equivalent internal structure as in N. timorensis does occur in *Nerinella grossouvrei* which according to COSSMANN (1898) was recorded in Hettangian (Lower Liassic) sediments. Therefore, the internal structure of the Nerineidae evolved latest in the early Jurassic. After BANDEL (1995), the ancestors of the Nerineaceans could be mathildoid gastropods of the family Anoptychiidae. Members of this family possess a heterostrophic protoconch, slender, cylindrical shells, flat whorls, a short anterior canal, and a slightly twisted columella.

There is no convincing argument against this opinion. It would merely mean that nerineaceans are polyphyletic. On the other hand, the number of plaits in *Melanioptyxis* is the same as in the Nerineidae. An origin of the Nerineidae from the same *Melanioptyxis*-like group as the Umboniidae and the Ptygmatidae therefore seems possible. In this scenario, the major nerineacean families could have evolved, perhaps unsynchronously, from the same ancestral group. In this case its pre-Jurassic history would still need to be clarified.

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Plate 1

Figures 1–6. *Adaptyxis lavdaris* n.gen.n.sp. Buzemadhe Hill, southeast Albania. Figure 1 shows the pillar within the central cavity.

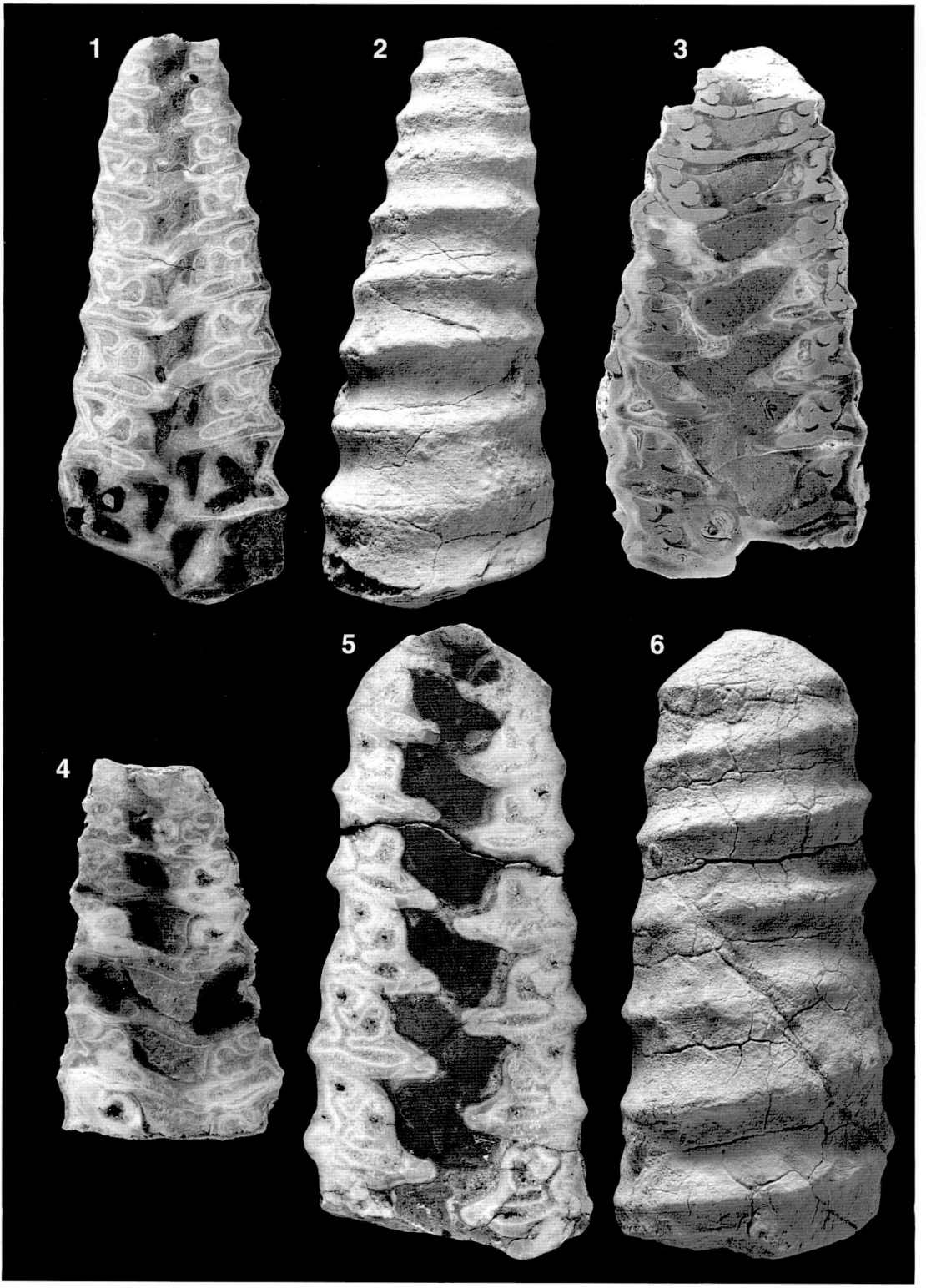
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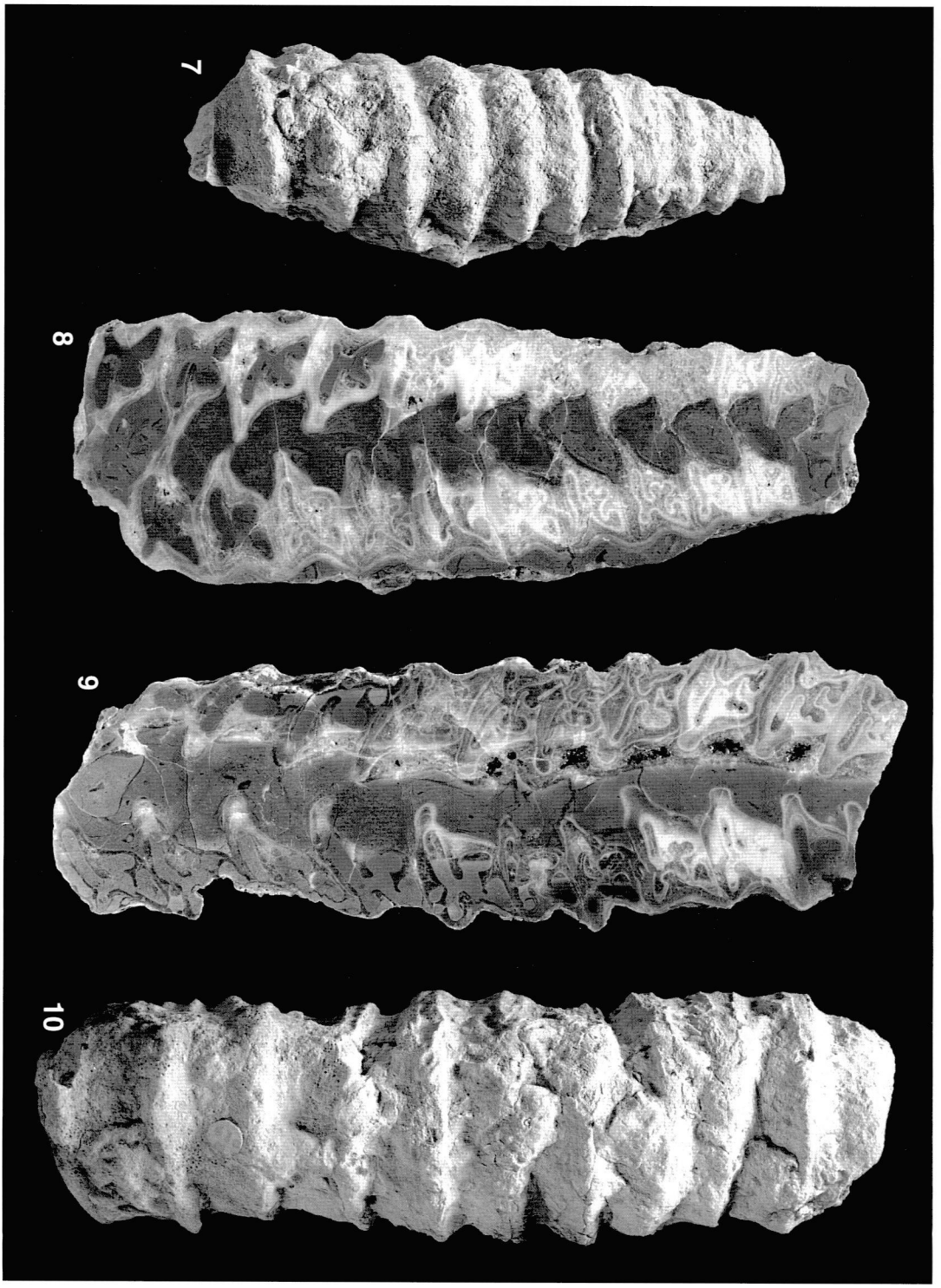
Plate 2

Figures 7–10. *Adaptyxis carinatus* n.gen.n.sp.

Photographs: Alice SCHUMACHER, Naturhistorisches Museum Wien. All figures in natural size.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